

Effects of starvation and mechanical manipulation of leaf litter on faecal pellet production and assimilation in some millipedes from southern Africa: Implications for feeding strategies

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Received July 6, 1992; accepted October 13, 1995

Abstract

Laboratory experiments were performed to establish the effects of starvation and mechanical grinding of leaf litter on the faecal pellet production and assimilation rates for three species of spirostreptid millipede common in the riparian savannas of south-eastern Botswana.

When food was present individuals produced between 6 and 20 faecal pellets per day. Starved animals stopped pellet production within 48 hours and retained some food in the gut. Individuals fed whole leaves, medium ground or fine leaf litter produced faecal pellets at similar rates but in *Zinophora* sp. the mass of individual pellets tended to increase with a decrease in food particle size. Assimilation rate of fine ground litter was independent of, and generally higher than the previous assimilation rate on medium ground litter.

The implications of starvation and intermittent pellet production on the evolution of digestive and foraging strategies in savanna millipedes and the effects of faecal pellet size on rates of decomposition are discussed.

Keywords: Diplopoda, feeding, faecal pellet production, assimilation, savannas.

Effets du jeûne et de manipulations mécaniques de la litière de feuilles sur la production de fèces et sur l'assimilation chez quelques espèces de myriapodes d'Afrique du Sud : implications dans les stratégies alimentaires.

Résumé

Des expériences de laboratoire ont été menées pour établir les effets du jeûne et d'un broyage mécanique de litière de feuilles sur la production de fèces et les taux d'assimilation chez trois espèces de myriapodes spirostrepsides communes dans les savanes riveraines du sud-est du Botswana.

En présence de nourriture, les individus produisent entre 6 et 20 pelotes fécales par jour. Des individus soumis au jeûne arrêtent la production de fèces pendant 48 heures et retiennent une partie de la nourriture dans leur tube digestif. Des individus nourris avec des feuilles entières, des morceaux de taille intermédiaire ou de la litière finement broyée produisent des fèces en quantités similaires, mais chez *Zinophora* sp., la masse de chaque pelote fécale tend à augmenter avec la diminution de la taille des particules alimentaires. Le taux d'assimilation était généralement plus élevé avec de la litière fine qu'avec des particules de taille moyenne.

Les implications du jeûne et de la production intermittente de fèces sur l'évolution des stratégies digestives et de recherche alimentaire des myriapodes de savane et les effets de la taille des pelotes fécales sur les taux de décomposition sont discutés.

Mots-clés : Diplopoda, nutrition, production de fèces, assimilation, savanes.

INTRODUCTION

In the savanna environments of southern Africa many biological processes such as litterfall (Malaisse, 1978) and decomposition (Campbell *et al.*, 1988) are strongly influenced by a highly seasonal rainfall pattern. Similarly many soil invertebrates are most active during summer when temperature and moisture conditions favour extensive foraging, dispersal and mate acquisition. Millipedes of the family Spirostreptidae emerge from the soil soon after the onset of the rains and begin to feed on a wide range of foods including leaf litter (Lawrence, 1984; Dangerfield & Telford, 1991; Dangerfield & Kaunda, 1994). In the drier savannas this surface activity is closely associated with intermittent rainfall events (Dangerfield, Milner & Matthews, 1993). During the wet summer the rainfall pattern is such that there are often dry periods of several weeks when few millipedes are surface active. Physiological constraints impose a limited tolerance to saturation deficits and individuals avoid extremes of stress in temporary burrows or other suitable refugia (Dangerfield & Chipfunde, 1995). In the dry winter months the animals aestivate in soil burrows or the vent systems of termitaria (Lawrence, 1984). Consequently, savanna millipedes encounter both long term starvation during the dry season and intermittent food shortages as a result of behavioral restrictions during the summer.

Tropical millipedes can occur at densities of 20 to 40 individuals m^{-2} (Toye, 1967; Dangerfield, 1990), exceptionally 800 m^{-2} (Bano & Krishnamoorthy, 1985) and in the spirosreptidae ingestion rates of up to 75 mg dry leaf litter per day (Dangerfield & Milner, 1993) can have a considerable impact on the available litter (Dangerfield & Milner, *in press*). For example, conversion of leaf litter to faecal material in miombo woodlands of Zimbabwe was estimated to be 18-28% of the annual litterfall, whilst the faeces themselves made up 12% of the litter standing crop (Dangerfield, 1993a).

Leaf litter in tropical savannas consists of material in various states of decay from whole leaves to fine fragments because of pulsed decomposition and slow turnover rates. In miombo woodland there is some evidence that the finer fractions decay more rapidly during the early part of the rainy season (M. J. Swift & S. Frost, unpublished data) which coincides with the peak of millipede surface activity and ingestion of litter. Millipedes feeding on leaf litter have the opportunity to select litter along this size continuum and may influence overall rates of litter decay.

In this paper experiments are described that begin to investigate the effects of 1) starvation and 2) particle size of leaf litter on faecal pellet production and assimilation in three species of spirosreptid millipede that ranged in body mass from 0.9 to 6.3 g. Only the physical effect of a reduction in particle size is considered in experiments using whole leaves that

were crushed, sieved and fed to millipedes in a palatability design. The results are discussed in terms of selection pressures acting on feeding tactics and the evolution of overall digestive strategies in savanna millipedes and the consequences of these strategies for litter decomposition.

MATERIALS AND METHODS

A) Study animals

Millipedes were collected from suburban gardens, roadside verges and riparian savanna in and around Gaborone, Botswana (24°40'S, 25°52'E) during October and November, 1990. Three species were used in the experiments: one member of the family Harpagophoridae, *Zinophora* sp. and two species of Odontopygidae, *Chaleponcus digitatus* (Attems) which was distinguished by a dark, almost black, body, red legs and red antennae; and *C. limbatus* (Attems) which has a dark body but yellow legs and antennae.

B) Basic design of feeding experiments

Faecal pellet production and assimilation were measured during feeding experiments in which individual millipedes were placed in 16 cm diameter plastic bowls and fed leaf litter *ad libitum*. Approximately 5 cm³ of water was added to all replicates every 3 days using a fine nozzle wash bottle and to maintain even humidity all bowls were loosely covered with a sheet of clear plastic. The number of faecal pellets produced was recorded daily for two months. All pellets were removed at each count for the first 14 days, thereafter were only removed after 28 and at the end of the experiment (58 days).

Faeces and any food remaining were air dried and weighed to permit gravimetric estimates of assimilation. Millipedes conserve moisture by producing very dry faeces and subsequent oven drying of selected samples at 60°C for 24 hours resulted in further moisture loss of less than 5%, hence air dry mass estimates were used in assimilation calculations.

Mass loss from leaf litter attributable to microbial activity was estimated and included in assimilation calculations. Three replicates of food additions per species (see below) were established, but with no animal present only mechanical disturbance at each addition of water. Mean mass loss from litter in these controls was $10.2 \pm 1.3\%$ (mean ± 1 s.e.; $n=13$), an amount subtracted from dry mass of food presented in each replicate prior to assimilation calculations. Further details of these procedures are given in Dangerfield & Milner (1993) and Dangerfield (1993).

C) Starvation experiments

At the start of the 1989-90 rainfall season female *Zinophora* sp. were collected from riparian savanna and established in a laboratory culture with excess leaf litter and ground rabbit pellets. Only females were collected due to a very low frequency of mature males in this population. Prior to the experiments a second group of females were collected, from which 40 were selected at random and each individual placed in a separate bowl. These females were denied food for 14 days during which time faecal pellet production was recorded.

On day 14 a further 40 females from the laboratory culture were transferred to individual bowls. These females and the starved group were each given 50 mg of commercially ground, white maize for 12 hours after which any remaining maize was removed. Ground maize is a readily accepted food source for millipedes and produces white faecal pellets in contrast to the brown or sandy colour of pellets from natural foods. The number and colour of pellets produced by both these groups of females was recorded for a further 10 days.

Cultures of *C. digitatus* and *C. limbatus* were also established at the start of the rainfall season from random field collections. In these species both males and females were collected and maintained separately in the laboratory. After three weeks in the cultures 14 individuals of each sex and species were transferred to separate bowls. Half these animals were starved and the other half were fed freshly fallen leaf litter from the canopy tree *Combretum erythrophyllum* (Burch.). The leaf litter was collected from riparian savanna in October and immediately dried at 60°C for 24 hours, mechanically crushed and passed through a 2 mm sieve. Faecal pellet production was recorded daily for 13 days after which the starved group were supplied with 0.8-0.9 g dry mass of leaf litter and pellet production recorded for a further eight days.

D) Food manipulation

The *Zinophora* sp. females fed ground leaf litter were used to assess the effect of mechanical grinding of food on faecal pellet production. Females from the starvation experiment and a further 20 from the culture were fed known quantities of crushed *C. erythrophyllum* litter that passed through a 2 mm sieve (medium) for 13 days during which time pellet production and mass of food eaten was recorded. After 13 days individuals were switched to either whole leaves (whole) or finely ground leaves that had passed through a 0.71 mm sieve (fine). Initially 5 leaves (approximately 1.0 g dry mass) were added to each replicate and 1.0 g dry mass of finely ground leaves. Daily pellets production and mass of individual pellets were recorded. The amount of food eaten and

mass of pellets produced were measured to estimate assimilation on both the medium and fine food.

Mortality of some female *C. digitatus* and *C. limbatus* during the starvation experiment reduced replication for these species to 5 females switched to fine food. Only assimilation and not pellet production rates was recorded for these females.

RESULTS

A) Starvation

Without food, faecal pellet production in female *Zinophora* sp. fell rapidly to less than 0.1 pellets day⁻¹ after 3 days (fig. 1). Some food was retained in the gut as when the maize meal was presented to starved animals pellets of the original food type, as well as white pellets from the maize, were produced by all individuals. Once the maize was removed pellet production again declined to less than 0.5 pellets day⁻¹ within two days (fig. 1). Pellet production in animals from the culture, who had previously had access to excess food, also fell sharply (fig. 1).

Similar patterns of pellet production on starvation were seen in *C. digitatus* and *C. limbatus* (fig. 2a). Differences between males and females were not

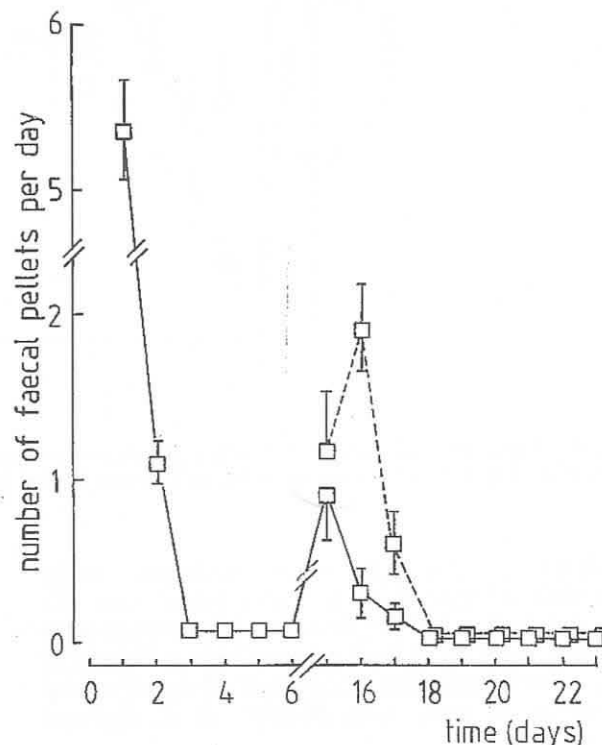


Figure 1. - Pattern of faecal pellet production in *Zinophora* sp. females during starvation (solid line) and females from laboratory cultures denied access to food (dashed line). Values here and in subsequent figures are means ± 1 standard error.

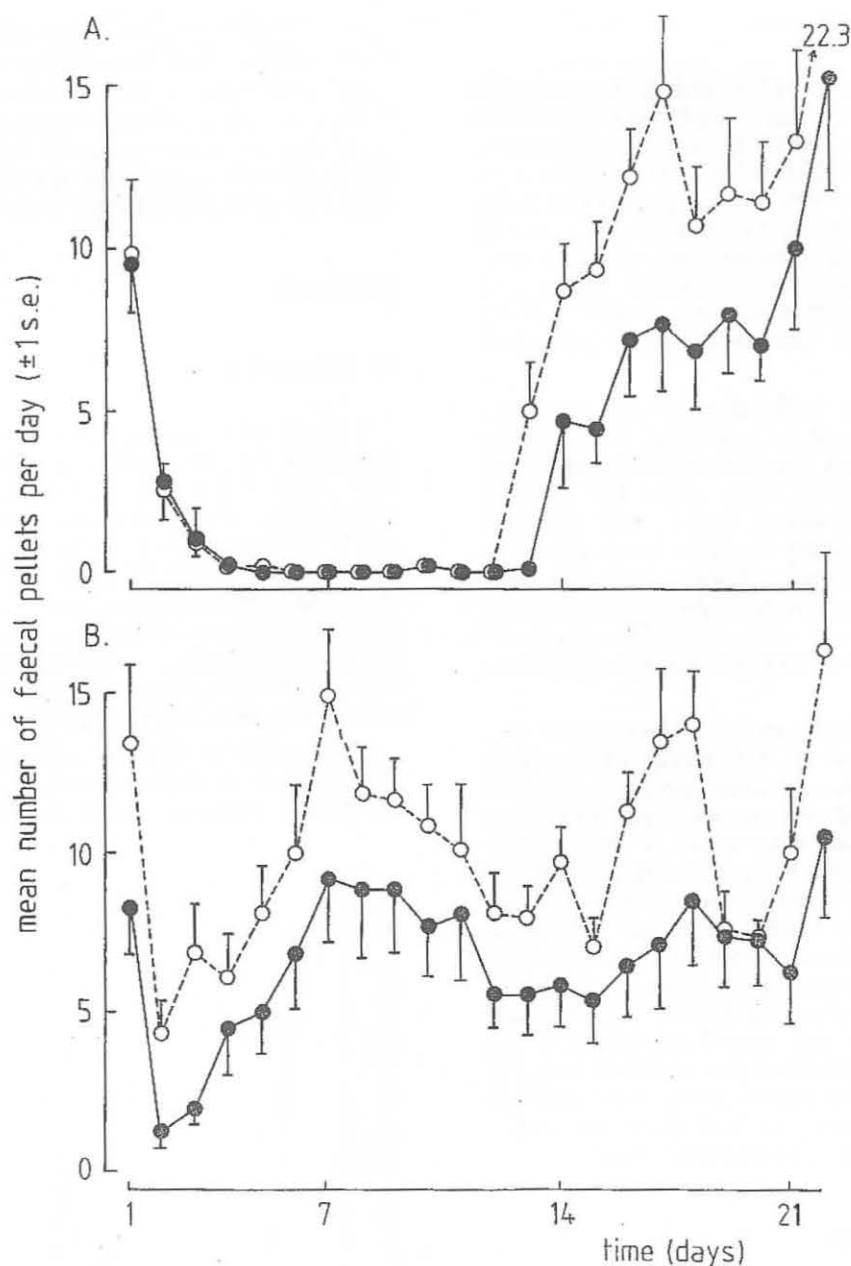


Figure 2. — Pattern of faecal pellet production in *C. digitatus* (open circles) and *C. limbatus* (closed circles) A) during starvation and subsequent feeding after 13 days and B) continuous feeding on *C. erythrophyllum* leaf litter ground and passed through a 2 mm sieve (medium).

significant so the data were combined. Pellet production declined from a higher initial rate, but more slowly than in *Zinophora* sp., and stopped after four days. As soon as food was available pellets were produced at an increasing rate for several days reaching an average of more than 20 day⁻¹ in *C. digitatus* (fig. 2a).

Individuals that had continuous access to leaf litter produced faecal pellets throughout the experiment (fig. 2b), although daily means differed greatly even

though the food was watered daily and conditions were standardised. It is possible that responses to changes in environmental conditions such as barometric pressure or air humidity affected the behaviour and feeding activity of individuals, even in the laboratory, which contributed to this variance. Inspection of pellet production rates for individuals suggest that some millipedes maintained steady rates whilst others showed distinct cycles of low and high production, perhaps reflecting periods of increased ingestion.

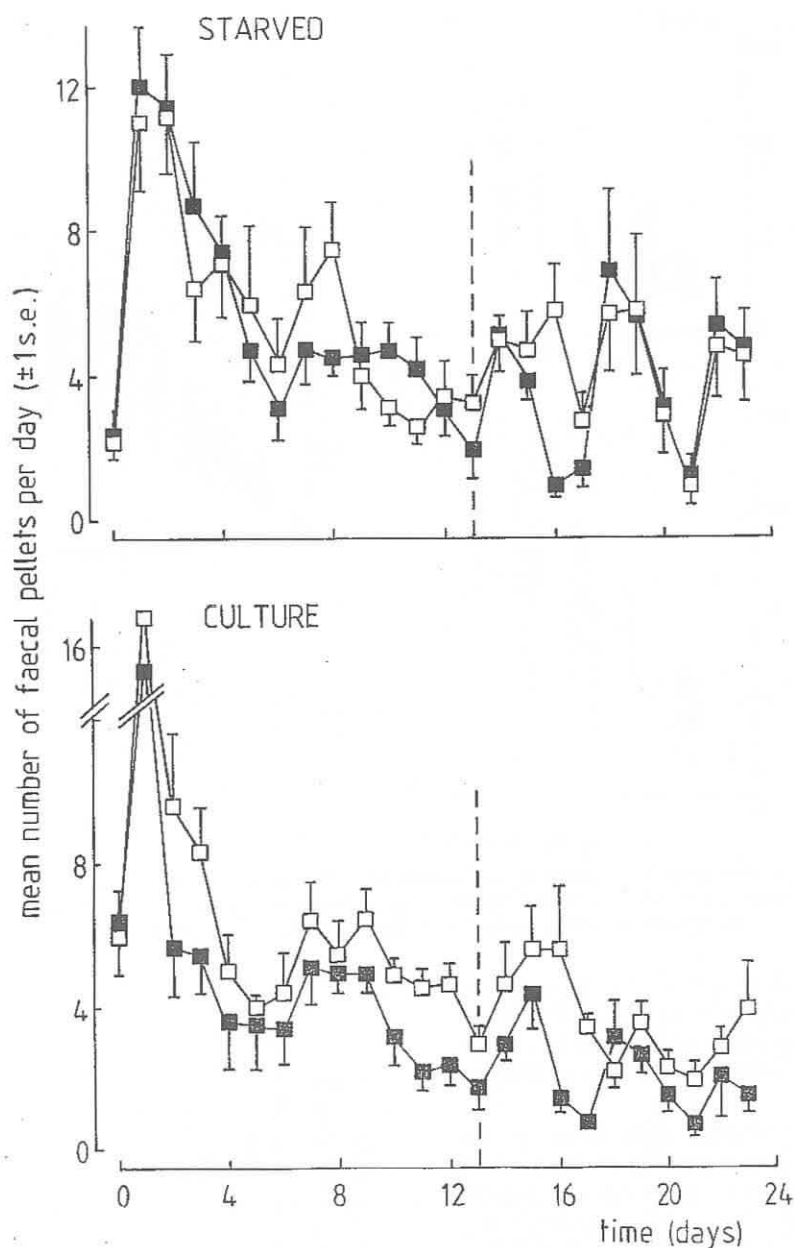


Figure 3. – Pattern of faecal pellet production in *Zinophora* sp. females, originally starved and originally with access to food in cultures, fed on medium ground *C. erythrophyllum* litter then switched to fine ground litter (open squares) or whole leaves (closed squares).

These cycles were not in phase between individuals but were of sufficient magnitude to affect overall means.

B) Mechanical manipulation of food

Female *Zinophora* sp. fed medium ground leaf litter initially produced numerous faecal pellets followed by a relative decline in production in both starved animals and those from laboratory cultures (fig. 3). Although constant, the artificial conditions in the experiments may have progressively influenced the feeding

activity of the animals through a restriction on normal burrowing and foraging behaviours. Effects of the change from medium to fine or whole leaves after two weeks on starved females was to increase variability in daily means but in females from the culture the decline in pellet production continued (fig. 3). Past feeding activity as well as immediate food availability appears to influence pellet production rate.

The mass of individual faecal pellets produced by *Zinophora* sp. females scaled positively with body mass with different exponents in the three food

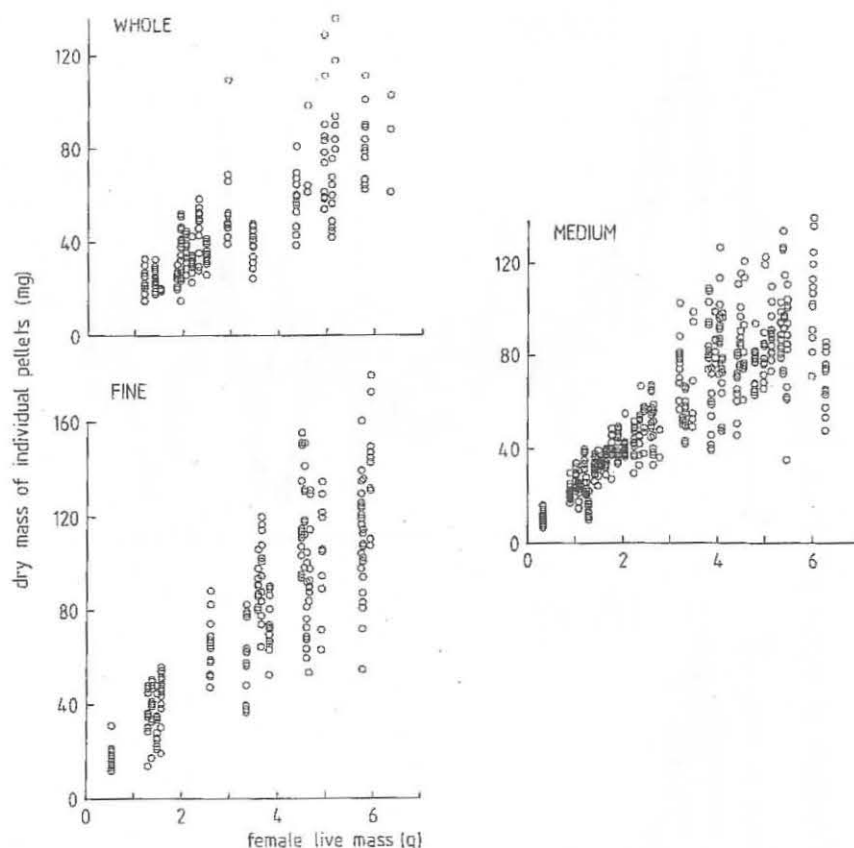


Figure 4. – Relationship between body mass (g live mass) and dry mass of individual faecal pellets in female *Zinophora* sp. fed A) medium ground leaves (0.71–2 mm), B) fine ground leaves (<0.71 mm) and C) whole leaves. Regression equations for pellet mass against body mass were for whole leaves; $y = 5.56 + 13.3x$, $r^2 = 61.5$; medium ground leaves, $y = 11.9 + 14.7x$, $r^2 = 72.7$; and fine ground leaves $y = 15.4 + 18.1x$, $r^2 = 67.8$.

treatments (fig. 4). A 5.0 g female fed fine ground litter would be expected to produce pellets that were, on average 34 mg (47%) larger than when fed whole leaves and 21 mg (24%) larger than when fed medium food.

Assimilation rates for female *Zinophora* sp. fed medium ground *C. erythrophyllum* litter were up to $7.5 \text{ mg g}^{-1} \text{ day}^{-1}$ but, on these gravimetric estimates, nearly half the females failed to assimilate any of this food type (fig. 5). However, once switched to fine food these females showed strong positive assimilation rates, whilst five individuals that had done well on the medium food were unable to maintain these rates on the fine material (fig. 5). Patterns for *Chaleponcus* species were less clear but more than half the individuals had higher assimilation rates on fine than medium food.

DISCUSSION

Starvation resulted in a rapid cessation of faecal pellet production and retention of food in the gut. Once food was available production of faecal pellets was almost immediate which supports the idea that food from previous feeding events is retained in the

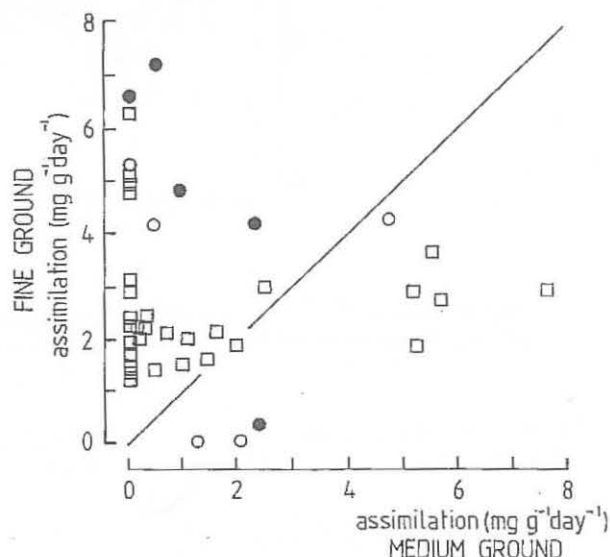


Figure 5. – Relationship between assimilation rates ($\text{mg g}^{-1} \text{ day}^{-1}$) of medium and fine ground *C. erythrophyllum* litter fed to female *Zinophora* sp. (open squares), *C. limbatius* (filled circles) and *C. digitatus* (open circles).

gut and suggests a simple digestive tactic of high throughput rates based on mechanical transfer through

the elongate gut structure. Bruggl (1992) found that in three temperate juliform species gut passage time is prolonged when the food supply is removed and shows a decline to zero in pellet production within 24 hours but does not state if any food is retained in the gut.

Food retention can be part of a digestion tactic to maximise assimilation efficiency (Sibly, 1981). However, prolonged gut retention of low quality foods is unlikely to enhance assimilation efficiencies because of diminishing returns on digestion of plant structural components. Most consumers of poor quality foods rely on high ingestion and throughput rates. Millipedes face a dilemma because advantages of high throughput rates only accrue when food is ingested. Peristaltic actions appear to have a limited capacity to effect food transport through the gut, and so inputs are required to maintain throughputs. In savanna millipedes food retention is an enforced tactic brought about by physiological constraints that limit feeding to certain favourable periods (see references in Introduction).

In effect, the extended and unpredictable periods when food is retained within the gut is also a constraint, but this time on the overall digestive strategy. Bulk feeding on poor quality material is only effective if throughput can be maintained, so natural selection would favour millipedes that choose the highest quality foods from those available and, therefore, benefit from occasional periods of prolonged digestion. Certainly the range of foods eaten by spirostreptid millipedes (Dangerfield & Telford, 1991; Dangerfield *et al.*, 1993; Dangerfield & Kaunda, 1994) is wider than previously recorded for temperate species (e.g. Wooten & Crawford, 1975; Kheirallah, 1979; Pobożny, 1986) and includes materials of relatively high quality such as dung, fallen fruits and seeds. Availability of such food types is often limited in time or else widely and heterogeneously distributed within the habitat. Preference for widely spaced food resources creates a selection pressure for greater mobility, an established advantage of large body size. Although present data are limited there is a hint that within the spirostreptidae there is a positive association between body size and a wider, more opportunistic food selection (Dangerfield, unpublished data). Certainly, large species such as *Alloporus uncinatus* (Attems) appear to select higher quality foods (*Acacia* seeds, fallen fruits, macrofungae) and also have the greatest surface activity (Dangerfield & Kaunda, 1994).

The mechanical manipulation of *C. erythrophyllum* litter had little effect on the pellet production rate of *Zinophora* sp. females but had a tendency to increase the mass of individual pellets. Observations here, and in previous studies on *A. uncinatus* (Dangerfield, 1993b), suggest that larger pellets tend to be more friable and, as such, would be less likely to persist in the environment. The effect of pellet size and textural composition on subsequent microbial activity and nutrient release remains to be investigated. McBrayer (1973) has shown that faecal pellets

from the temperate enchytraeid *Apheloria montana* (Bollman) have smaller particle sizes, increased pH and greater moisture than ingested food. This favours increased microbial activity and provides a competitive advantage to bacteria over fungi, both of which would enhance decomposition rates. An increase in pellet size may also improve moisture holding capacity but this may be counteracted by the reduced cohesion of the material. Data for *Glomeris marginata* (Villers) suggest no difference in rates of decomposition between faecal pellets and leaf litter (Nicholson, Bocock & Heal, 1966) whilst, in the absence of roots, there is an accumulation of available nitrogen in faeces of *Pachyiulus flavipes* (Koch) compared with leaf litter (Striganova & Chernobrovkina, 1992). Tajovsky (1992) also showed a doubling of microbial activity in faeces of *Glomeris hexasticha* (Brandt) compared with leaf litter, a pattern also observed previously in *G. marginata* (Anderson & Bignell, 1980; Hanlon, 1981). These observations suggest that faecal pellets should decompose faster than leaf litter but more detailed studies are required, particularly under field conditions.

Soma & Saito (1983) in experiments on the ingestion and assimilation of pine needles by the woodlouse *Porcellio scaber* (Latreille) used whole and powdered needles and found little difference in assimilation with powdered material but a significant increase in ingestion of the less well decayed material. A similar result of increases in ingestion without appreciable increases in nett assimilation has been recorded for the woodlouse *Armadillidium vulgare* (Latreille) (Cameron & LaPoint, 1978). In the present study assimilation was greater when the animals were fed finely ground food but this was not a clear trend, notably in *Zinophora* sp. females where high assimilation on medium ground food resulted in poor assimilation when switched to fine food (fig. 4). A further complication under field conditions is that the fine litter fractions would be of different nutritional status due to their advanced stage of decomposition, not a parameter considered in these experiments. Millipedes do consume significant amounts of soil which in some species is related to consumption of algae (Dangerfield *et al.*, 1993) but in others suggests a preference for finer litter fractions that are inevitably mixed with mineral soil (Kheirallah, 1979; Dangerfield, 1993b). Such preferences are likely if assimilation efficiencies are greater and may be responsible, at least in part, for the loss of smaller size fractions from the litter standing crop during the early part of the rainfall season.

Although apparently trivial, breaks in faecal pellet production and retention of food in the gut becomes a constraint to the overall feeding strategy and could contribute, through diet selection, to an evolutionary pressure for large body size. Similarly, pulsed feeding patterns by millipedes and a preference for certain litter fractions are likely to influence rates and timing of litter decomposition in savannas.

Acknowledgement

This work would not have been possible without the laboratory assistance of Alice Milner.

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